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The TERMINATION *of the* NERVES *in the* VESTIBULE *and* SEMICIRCULAR CANALS *of* MAMMALS.

Read before the British Association, Glasgow, September, 1876, by URBAN PRITCHARD, M.D., F.R.C.S., Aural Surgeon to King's College Hospital, Lecturer on Animal Physiology, King's College, London. (With Plate XXVIII.)

IN this paper I propose giving the results of my investigations into the structure of the nerve-epithelium, as it is called, which contains the terminal distribution of the acoustic nerves in the vestibule and semicircular canals.

Up to the present this structure has been chiefly studied in the cold-blooded vertebrates and birds; and the various observers (including Max Schultze, Kölliker, Odenius, Hasse, Rüdinger, Ebner, and Meyer), although they agree as regards certain general points, yet appear to differ considerably respecting many important questions.

Having been fortunate enough to make some very successful preparations of this nerve-epithelium in the adult and fœtal cat, which to my mind throw considerable light on the subject, I have ventured to lay before you the results of these observations.

The area of distribution of the acoustic nerve in the vestibule and semicircular canals is limited to five spots,—one situated respectively in each division of this part of the membranous labyrinth; namely, the Saccule, Utricle, and three ampullæ. In the latter the area of distribution is raised into a kind of ridge or crest, and for this reason was named by Max Schultze the Crista Acustica; whereas in the Saccule and Utricle it is merely an oval spot, and has received the name of the Macula Acustica from the same author.

In the region of these acoustic ridges and spots the membranous labyrinth is firmly adherent, by means of a layer of dense connective tissue, to the bony wall, not being separated by the epilymph as in other parts of the labyrinth, and the membrane itself is specially modified in structure.

Speaking generally this membrane consists of three parts; externally an irregular layer of loose connective tissue; next a dense layer of the same tissue, frequently called the Tunica Propria; and lastly a single layer of tesselated epithelial cells. At the acoustic spots the outer layer is lost, becoming blended with the periosteum, which in many animals (sheep, guinea pigs, &c.), here presents a layer of branched pigment cells, such as are found in the choroid coat of the eyeball. The tunica propria remains almost unchanged, but in the epithelial layer are to be found some very remarkable modifications.

The tesselated cells as they approach the acoustic spot gradually increase in thickness, and become first cuboid and then columnar, in which form they are found on the margin of the acoustic spot, where they are changed into nerve-epithelium. But before proceeding to the detailed account of this structure, I must mention that scattered somewhat irregularly amongst the columnar epithelium are found (according to Hasse, Odenius, and Meyer), peculiar pigmented fibro-granular cells with small summits and extending bases, which frequently meet, giving the appearance of a pigmented network when looking at the membrane from above; these cells appear to be similar to those found so abundantly in the tegumentum of the bird's cochlea.

The Nerve-Epithelium.

Max Schultze in 1858 described this structure in the fishes as consisting of three epithelial forms. A deep layer of nuclei which comes next to the tunica propria, these he called the Basalzellen; a superficial layer of cylindrical cells, Cylinderzellen; and numerous nuclei between them, surrounded by protoplasm and having prolongations upwards and downwards, the former passing between the cylindrical cells, and the latter between the nuclei of the lower layer, —these middle cells he termed Fadenzellen. He admitted that he was unable to trace the exact origin of the cilia which project from the epithelial layer.

Odenius, Kölliker, and Max Schultze himself, in his later researches, found similar structures in the higher animals; and although they differed somewhat in details, yet they came essentially to the same results.

Hasse, in his earlier researches on the bird, found himself unable to corroborate the statements of Max Schultze, and he described the nerve-epithelium as consisting of two alternating forms of almost cylindrical epithelial cells. The one bearing the cilium he very aptly terms the thorn cell, and the other the isolating cell.

The thorn cells he describes as being fusiform, with the thorn projecting from its upper part; the isolating cells as enlarged at their base, which contains nuclei and rest on the tunica propria, the upper part of the cells being narrow, and passing between the thorn cells so as to separate them.

Rüdinger, in his description of this structure in 'Stricker's Histology,' somewhat reverses Hasse's statement, and depicts it as consisting of fusiform ciliated cells alternating with triangular ones, with their bases turned upwards instead of downwards. At the same time he states that he has been unable to discover the deep layer of nuclei described by Max Schultze.

Ebner, in endeavouring to reconcile the opposing statements of Max Schultze and Hasse, came to a conclusion which differed from each. He considers that this nerve-epithelium consists of two parts—a superficial layer of cylindrical ciliated cells with a cuticular border above, and rounded off below, and layers of fusiform cells made up of a nucleus and two fine prolongations, the upper one passing between the cylindrical cells as far as the cuticular border. The nuclei of this second set of cells correspond to the deep layer of Max Schultze.

Lastly, Meyer, in his elaborate work on the membranous labyrinth, just published, arrives at very different results. He describes a deep layer of nuclei, as Max Schultze, and above this a layer of cylindrical cells, with cilia projecting from their upper free ends, and abruptly tapering to a nerve filament below.

My observations have led me to conclusions which, although they are essentially different from those of the authors just alluded to, yet appear to me to reconcile, to a great degree, their various conflicting descriptions.

As this structure is admitted by all observers to be virtually the same in the vestibule and ampullæ, a description of the macula acustica of the saccule will suffice for all.

Figs. A, B, and C (Plate XXVIII) represent a transverse section of the macula at different points, and is drawn from a preparation of the labyrinth of a cat ten months old.

A glance at the drawing will suffice to show that this nerve-epithelium does not present the same appearances throughout the whole macula. I therefore propose, first, to describe the type of this structure, and then its modifications.

A typical portion, such as may be seen midway between the centre and circumference of the spot, consists of a row of alternating elongated cells, bordered by a distinct cuticular membrane. Below these is a nuclear layer, such as has been described by all recent observers with the exception of Rüdinger; however, connections may be clearly traced between the upper elongated cells and this deep layer of nuclei; so that the cellular elements of this tissue may be described as consisting of two alternating forms of elongated cells, each having an upper and a lower nucleus.

The first I call the thorn-cells, on account of the shape of their cilium, and the second the bristle-cells, for a similar reason.

The thorn-cells have a fusiform body, containing an oval nucleus; from this body passes upwards a single cilium, which gradually tapers to a point; this cilium or thorn passes through an opening in the cuticular membrane, but appears to be totally unconnected with it. The lower tapering extremity of the body passing downwards again expands and encloses a second oval nucleus.

The bristle-cells have a triangular body containing an oval nucleus; the base of this is intimately connected with the cuticular membrane, and from this base passes upwards a single narrow cilium or bristle, having parallel and not tapering borders, thus resembling in shape, though much larger, those found on the ciliated cells of Corti in the mammalian cochlea. The apex of this triangular body is prolonged downwards, and has a second enlargement containing a second oval nucleus; this is usually situated at a different level to that of the corresponding enlargement of the thorn cell, and thus the alternating cells appear to dovetail, as it were.

The cuticular membrane is a very thick, well-marked membrane, keeping the cellular elements in their place, and perforated for the passage of the cilia. I am very much surprised that none of the previous investigators should have described this membrane; it is true that Ebner and Meyer hint at something of the kind, but the other authors appear to ignore it entirely. I can only account for this by the fact that in fœtal preparations this membrane cannot be made out.

This cuticular membrane is undoubtedly analogous to the reticulate membrane of the organ of Corti, and I therefore propose calling it by the same name—membrana reticularis.

Having described the type of the nerve-epithelium, I now pass on to its modifications. As there is a general increase in the thickness of the macula from circumference to centre, so the cells and their various parts elongate; the cilia, which are short and stumpy at the edge, become very much longer and comparatively finer at the centre of the acoustic spot.

Round the border of the spot the cells pass by insensible gradations into the columnar form of the epithelial cells which surround it. In this change the double nature of the cellular elements is very apparent.

Towards the centre of the acoustic spot the upper nucleus and surrounding protoplasm of the bristle-cells gradually diminish, and then are lost altogether, the cell being represented by a trabecula from the membrana reticularis, tapering downwards towards its second or lower nucleus. The bristle-like cilium remains after the upper protoplasmic mass has disappeared, but eventually this also is lost. Curiously enough, as this atrophy of the cell is proceeding, the bristle-like cilium appears to go out of its course to approach nearer and nearer to its neighbouring thorn, so that towards the centre of the acoustic spot the two cilia are seen lying close together, and almost appear to proceed from one and the same cell.

I think this description bears out what I just stated, that my observations tend to reconcile the opposing views of previous writers.

Naturally, the lower layer of nuclei has been recognised by all except Rüdinger, who seems to have been unfortunate on this point.

The isolating cells of Hasse and triangular ones of Rüdinger are represented by my bristle-cells, no one having previously observed their cilia, or, indeed, that there were two forms of cilium. Again, these cells, where they lose their upper nucleus, correspond to the filiform cells of Max Schultze and Ebner.

Rüdinger's description is very like what may be seen in fœtal preparations, where the cells retain much of their original epithelial form.

My thorn-cells correspond to the cylindrical or fusiform ciliated cells recognised by all.

The Nerves of the Maculæ and Cristæ.

Having thus fully described the nerve-epithelium, I now pass on to the nerves themselves, and will afterwards briefly describe the otolith mass covering the acoustic spots.

The vestibular or posterior division of the portio mollis separates into five branches, one for each of the areas of distribution. In the trunk of this nerve and its branches, but especially in the former, are found fusiform bipolar ganglion cells, corresponding to those of the ganglion spirale of the cochlea, but much larger, those of the latter averaging $\frac{1}{1000}$ inch in length, whilst the vestibular cells average $\frac{1}{600}$ inch.

These five branches pass through the bone to their respective destinations, and the fibres arriving at the membrana propria lose their white substance, entering the nerve-epithelium without it. After passing this point there is considerable difficulty in tracing the nerve filaments, but the later observers are all agreed, as no doubt is the case, that they found a plexus around the deep layer of nuclei, and that some of the filaments may be traced directly or indirectly into the ciliated cells. Meyer describes and figures minute nerve filaments forming a plexus and passing up between the cylindrical cells; the existence of these has not as yet been confirmed by my observations.

Rüdinger states that he has traced the nerve filament through the centre of the ciliated cell and its nucleus right to the cilium itself; I have sometimes fancied that I could also do this, and certainly there is a central darker portion to be seen in the thorn-shaped cilia.

The Otolith Mass.

Covering the acoustic spot is a soft mass of cuticular tissue, into which the cilia project to a certain distance. This mass has an irregular reticulate appearance in preparations, but is evidently of a cuticular nature and analogous to the membrana tectoria of the cochlea, with which it is continuous in the bird according to Hasse. The otoliths are fixed by this mass, being chiefly contained in its outer portion.

In conclusion, I would observe that, although I am confident that my explanation of this structure is the correct one, and, further, that I can satisfactorily demonstrate most that I have put forward, yet further research is needed to render the matter more certain, and especially to clear up the question of the ultimate termination of the nerve filaments.

The following is the list of authors' works referred to; and to those who may be desirous of entering more fully into the history of the subject I would specially recommend the work of Paul Meyer on the 'Labyrinthe Membraneux,' just published.

Max Schultze.—'Ueber die Endigungsweise des Hörnerven im Labyrinth,' 1858. J. Müller, 'Archiv für Anat. u. Phys.'

Kölliker.—'Handbuch der Gewebelehre des Menchen,' 1867.

M. V. Odenius.—'Ueber das Epithel der Maculæ Acusticæ beim Menschen,' 1867. 'Archiv für Mikros. Anat.'

C. Hasse.—"Der Bogenapparat der Vogel," Siebold u. Kölliker, 'Zeitschr. für Wissensch. Zoologie,' Bd. xvii, p. 381.

C. Hasse.—'Das Gehörorgan der Fische.' Idem, p. 454.

Rüdinger.—'Stricker's Histology,' vol. iii.

Ebner.—"Das Nerven-Epithel der Cristæ Acusticæ," in 'Schriften des Med. Natur. Wissensch. Vereins zu Innsbruck,' 3 Jahrg., 1872.

Paul Meyer.—'Etudes Histologiques sur le Labyrinthe Membraneux,' 1876.

EXPLANATION OF PLATE XXVIII,

Illustrating Dr. Pritchard's paper "On the Termination of the Nerves in the Vestibule and Semicircular Canals of Mammals."

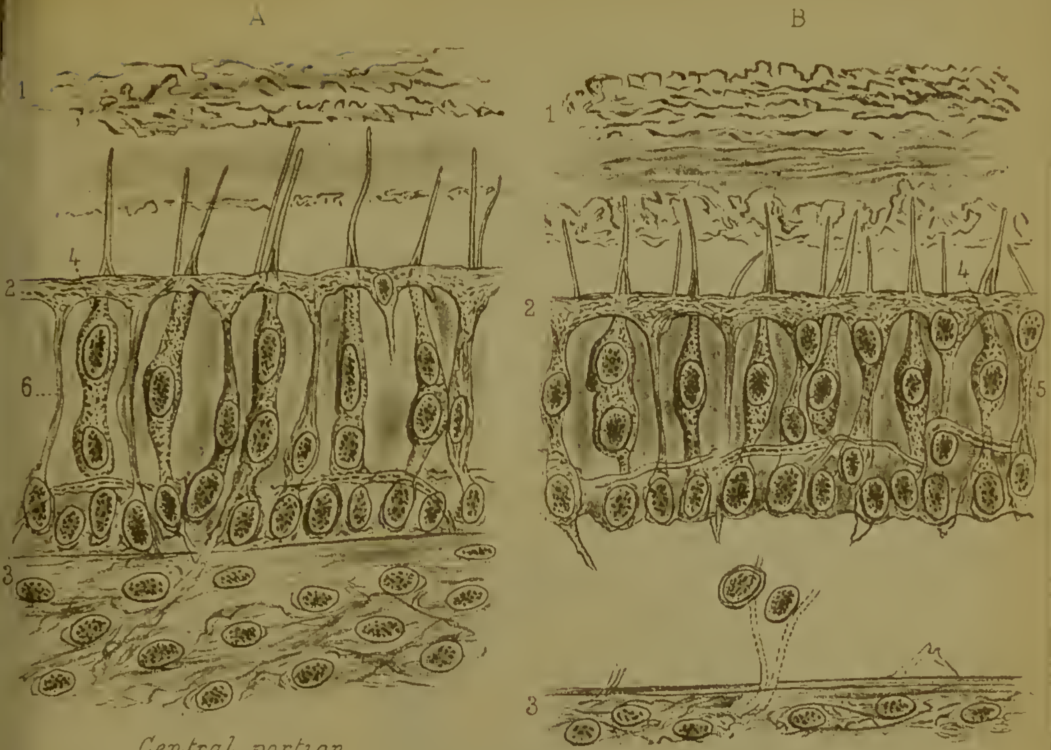
Portions of a transverse section through the macula acustica of saccule of cat, ten months old. × 750 dia.

A. Centre of macula. Otolith mass above, into which the long cilia are projecting; the otoliths themselves having been dissolved out. Nerve-epithelium, lying on the modified periosteum, consists of thorn-cells and atrophied bristle-cells kept in position by the membrana reticularis.

B. Intermediate portion. Otolith mass as before, cilia not so long. Thorn-cells as before; bristle-cells perfect towards the outer side, atrophying towards the inner. Nerve-epithelium has been separated by accident from tissue beneath, whence nerve-filaments are seen passing upwards.

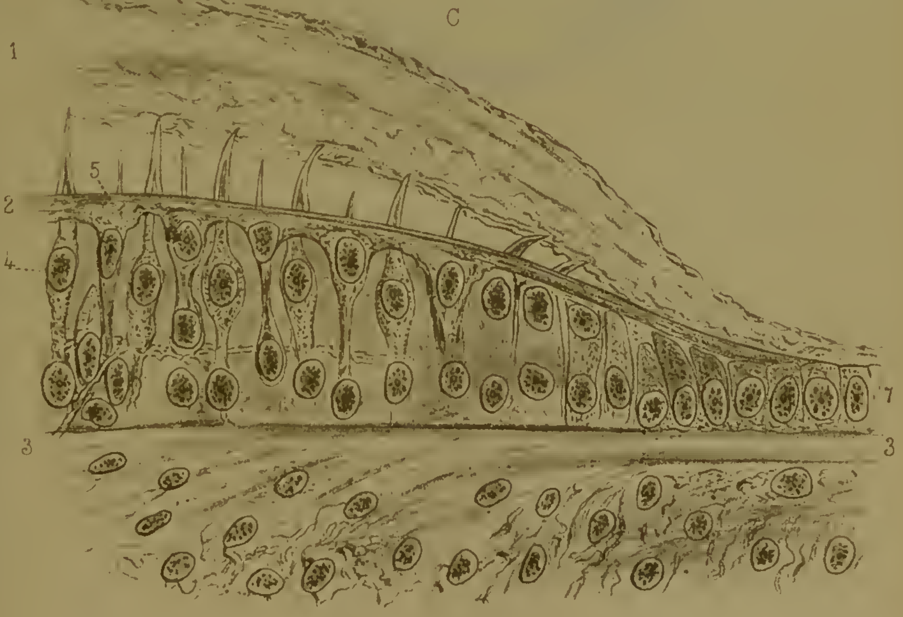
C. Edge of macula. Otolith mass thinning off towards the columnar epithelium, cilia short and stumpy. Membrana reticularis becoming gradually lost. The nerve-epithelium changing by degrees into ordinary columnar cells.

1. Otolith mass. 2. Membrana reticularis. 3. Membrana propria, blended with periosteal tissue beneath. 4. Thorn-cells. 5. Bristle-cells. 6. Atrophied bristle-cell, now forming a trabecula from membrana reticularis. 7. Columnar epithelium surrounding macula.



Central portion

Intermediate: separated accidentally from osseous wall.



Edge of Macula

Urban Pritchard

P.H. Miller, del^t

M^c Farlane & Erskine Lith^{rs} Edin^r

SECTION THROUGH MACULA ACUSTICA OF SACCULE OF CA

X 750 *Diameters*

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